conversion between the unfolded and the folded forms has also been monitored[8]: with a folding time-constant of around one second, unfolded protein molecules can presumably reorganize themselves to bind a target peptide rapidly enough that peptide binding and signal transduction are not impeded.

If the biological activity of unfolded proteins turns out to be a widespread phenomenon, how do these proteins escape degradation and aggregation in the cell? It is quite possible that unfolded yet active proteins can only occur on the cell surface, or in roles where they are found only at low concentrations in the cell — as with FlgM, which is either exported or bound to σ^{28}.

The awakened interest in the unfolded state corresponds with a 'new view' of protein folding[9]. This replaces the models of discrete folding pathways by multipathway 'energy landscapes' and defined intermediates by a distribution of partially folded conformations. Studies of unfolded proteins, both by NMR and by Monte Carlo simulations, have converged on the view that unfolded proteins sample backbone conformations that are remarkably similar to those found in fully folded proteins[10]. This presumably biases the conformational search that is undertaken by the polypeptide chain during folding, and is one of the mechanisms by which folding can avoid the astronomically long times that the Levinthal paradox predicts for a random search mechanism.

New evidence for the biological relevance of unfolded states has also arisen from studies of pathogenic proteins. Unfolded conformations seem to be critically involved in the transformation from normal to pathogenic forms of the prion, and of proteins that are implicated in amyloidosis-related diseases such as Alzheimer's[11,12]. We anticipate that future developments in this field, together with the insights gained from the 'new view' perspective, will lead to a more widespread appreciation of the idea that proteins are dynamic systems, sensitive to evolutionary modulation even in their unfolded conformations. □

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Climate change

A greener north

Inez Fung

For whatever reasons, the period since 1980 has been the warmest in the past 200 years. Every gardener can speculate about the fate of his garden in response to the warming, but the bigger question is whether the biosphere has responded in some larger way to the climate perturbation. Sustained long-term observations of photosynthesis are rare. Furthermore, the biosphere is notoriously heterogeneous. It is very difficult to extrapolate from field measurements at a few sites to behaviour over a large region.

On page 698 of this issue[1], Myneni *et al.* present satellite evidence that, on average, the biosphere between 45° N and 70° N has been enjoying increased photosynthesis between 1981 and 1991. The authors suggest that temperature increases in the spring time have also brought a longer growing season to the high latitudes. The evidence presented by Myneni *et al.* is the first direct observation of the biosphere that photosynthesis has increased on such a broad scale for such a long time. The satellite observations are extremely provocative and, the authors argue, reveal specific areas where changes have occurred.

Remote sensing of photosynthetic activity is based on how plants use or dispose of solar radiation at different wavelengths. Green leaves absorb more than 85% of the incoming solar energy in the visible part of the spectrum and under 40% of the energy in the near-infrared: hence there is a large difference between the reflectivities at these wavelengths. By contrast, the reflectivities at these wavelengths are comparable for bare soils. A commonly used parameter for monitoring photosynthetic activity is the normalized difference vegetation index (NDVI): the difference between the reflectivities at the two wavelength bands normalized by the sum. A high NDVI is indicative of vigorous photosynthetic activity.

Satellite observations provide a global view of the land surface in days to weeks, depending on the days without clouds to obscure the view. The pioneering work of Tucker and his co-workers[2,3] has demonstrated the usefulness of the NDVI for deducing vegetation classes on a continental scale and for monitoring photosynthetic activity on a global scale. These studies employed satellite observations for a single year or a few years, and centred on the spatial and seasonal information contained in the NDVI distributions.

Looking for long-term changes in the satellite data is a challenge. The instruments were designed for weather applications in which the time scale of interest is days. The 11-year NDVI time series have been constructed from data from three radiometers on board three different polar-orbiting meteorological satellites. The performance of the radiometers diminishes with time, and at different rates for different wavelength channels. Furthermore there is the annoying interference by the intervening atmosphere. By selecting the maximum NDVI value over a period of 10 or 15 days, one hopes to have avoided clouds, which, being reflective in the visible spectrum, would yield a low NDVI. Also, because of the satellite viewing and solar geometries, there are differing amounts of atmosphere between the sensor and the surface; more importantly, the abundance of other atmospheric constituents (aerosols, for example) that interact with the radiation is not uniform in space or time. These must be removed before a clean signature of the surface can be obtained.

Myneni *et al.*[1] have taken a bold new step forward in extracting a secular trend from the NDVI information. They used two NDVI datasets, independently derived from the same raw satellite data. Each dataset includes a *post facto* correction for instrument calibration and atmospheric effects. As the authors point out, the correction is not complete, but they are confident that the NDVI trend at high latitudes is robust. For similar reasons, they have refrained from interpreting the trends in the tropics.

Should we believe in the NDVI trend? There are no 'ground-truth' measurements of photosynthesis at northern high latitudes over the same period, and so the accuracy of the trend cannot be established unambiguously. Nonetheless, the consistency between the two independently processed NDVI datasets inspires some confidence. For corroboration, the authors present Keeling and colleagues' finding[4] of an increasing trend in the amplitude of the atmospheric CO_2 annual cycle at Point Barrow, Alaska.

Photosynthesis removes CO_2 from the atmosphere. Carbon is returned to the atmosphere through respiration of microbes decomposing dead organic matter. The different timing in the photosynthesis and respiration gives rise to an annual cycle of CO_2 in the atmosphere. Over the tropical rainforests, where inhalation and exhalation of CO_2 are large but nearly cancel over a day to a month, there is little seasonal variation in atmospheric CO_2. The largest amplitude of the CO_2 annual cycle is found at high latitudes in the Northern Hemisphere, where the growing season is short and photosynthesis and respiration are asynchronous. The positive trend in CO_2 amplitude is evidence of a consequence of increased biospheric activity, but not direct evidence of the increased activity itself. The trend in photosynthesis presented by Myneni *et al.* is thus only part of the story of the trend in CO_2 amplitude. Increased temperatures are likely to have stimulated both photosynthesis and respiration, and/or changed the phasing between the two.

What does the NDVI trend mean for the contemporary carbon budget? Again, whether the carbon inventory in the biosphere has increased or decreased over the past 15 years depends on the competition between photosynthesis and respiration. The latitudinal gradients of CO_2 and its isotopes point to a repository of anthropogenic CO_2 in the terrestrial biosphere at northern middle to high latitudes[5–8]. These inferences, on top of the NDVI and CO_2 amplitude trends, suggest that photosynthesis has won over respiration at northern high latitudes.

It will be a challenge for ecologists to explain how photosynthesis could have increased by some 10% from 1981 to 1991. Over the same period, the increase in CO_2 levels is only 4%, from 340 p.p.m.v. to 355 p.p.m.v. (parts per million by volume), and could not have enhanced photosynthesis at the NDVI rate. Temperature increases may have stimulated photosynthesis directly, or accelerated snowmelt and mobilized nutrients previously frozen in soils. The magnitudes of these effects remain to be investigated.

With the revelation, from ice-core data, of the roller-coaster fluctuations of climate, one cannot help but wonder how the biosphere has fared in the ride. Fossil pollen records show recurring rearrangements of the seating in the past. Myneni and colleagues' study provides evidence that the biosphere, at least at northern high latitudes, has been an increasingly restless passenger in recent years. Other studies[9] suggest that the biosphere, even without rearrangement, may not be a passive passenger but may feed back on the climate change.

In 1998, NASA is scheduled to launch AM-1, the first platform of the Earth Observing System (EOS). Instruments on board AM-1 promise to be calibrated, and simultaneous observations of aerosols and other atmospheric constituents will allow for a careful removal of atmospheric effects. What new insights into our backyards will be revealed by the forthcoming satellite observations? □

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Population biology

Hosts and parasitoids in space

H. C. J. Godfray and M. P. Hassell

Parasitoids are insects whose larvae develop on or in the body of other insects, eventually killing them (Fig. 1). Their population dynamics have been studied intensively, both because of their economic importance in controlling pests, but also because they provide a relatively simple system for investigating dynamic processes common to all consumer–resource interactions.

In recent years, theorists have been exploring how an explicit consideration of space affects the dynamic interactions between hosts and parasitoids, a move that reflects an increasing realization of the importance of spatial processes in all branches of population dynamics. But although the mathematical models reveal a fascinating menagerie of dynamic patterns, experimental studies have lagged behind, chiefly because of the great logistical problems involved. However, a series of studies, including that of Roland and Taylor on page 710 of this issue[1], have demonstrated the rewards of taking a spatial approach.

Roland and Taylor studied a moth called *Malacosoma disstria*, the forest tent caterpillar, which feeds in aspen woodland in central Canada. The moth's caterpillars live gregariously in silken webs, and can become common enough to defoliate large areas of forest. Although the population dynamics are not wholly understood, it is thought that outbreaks are suppressed by parasitoids of the moth, particularly certain flies of the families Tachinidae and Sarcophagidae.

Before human intervention, aspen forests occurred over wide areas, but today they have been fragmented into stands of varying size. Roland and Taylor asked how fragmentation and host density influence the pattern of attack on *M. disstria* by the different species of parasitoid. They sampled populations of the moth and parasitoid at 127 sites within a 25×25 km grid, and repeated the exercise at 109 sites within a smaller 800×800 m grid. Employing statistical modelling techniques, they then sought to explain observed rates of parasitism by each of four species of parasitoid using two classes of explanatory variable:

A. LE MASURIER

Figure 1 **Parasitoid attack — here a brood of the braconid wasp *Cotesia glomeratus* emerges from the caterpillar of a small white butterfly, *Pieris rapae*, before undergoing pupation.**